NORTH AMERICAN TREES WITH RELATIONSHIPS IN EASTERN ASIA

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ABSTRACT

Much information on distribution and taxonomy of North American trees with relationships in eastern Asia, including atlases and monographs, is now available. Eastern Asia is the world's largest and richest source of temperate deciduous hardwoods. Because of splitting of genera and species, relationships are becoming obscured and are primarily generic. Eastern Asia is the geographic region or center with greatest display of remnants of the widespread Arcto-Tertiary flora, while Eastern North America is second, with roughly one-half as many tree species. Europe and Western North America have smaller numbers, perhaps one-fourth. Many tree genera are widespread in all four regions. Most of the possible patterns of distribution are represented. Eastern North America and Eastern Asia have the most tree genera, about 16 in common. The relationships have been overemphasized. They are readily explained by mountain-building and changes in climate, especially Pleistocene glaciation.

A review of temperate North American trees with relatives in Eastern Asia is timely. Much information on distribution and taxonomy, including atlases and monographs, is now available and because of expanded markets for hardwoods there is increased interest in foreign trees for introduction in forestry as well as in horticulture. Also, the relationships among tree genera in North America and eastern Asia are becoming obscured, because of splitting of genera and species. The main conclusions are that these relationships have been overemphasized and are readily explained by earth changes accepted within recent years.

Trees, though an artificial group of large woody plants, are excellent examples for biogeographical studies. They are large, conspicuous, relatively well known, of moderate numbers of species, and of economic importance. Thus, their classification has been studied in detail, and their geographic distribution has been mapped. Also, they are preserved as fossils and have a historical record, though with many gaps.

Review of literature. Certain similarities in the floras of temperate Eastern North America and Eastern Asia have long attracted the attention of botanists. These observations have been traced back to Carolus Linnaeus in 1750, Carl Pehr Thunberg in 1784, Luigi Castiglioni in 1790, and Asa Gray (Graham, 1972). Asa Gray (1840, 1846, 1859, 1873, 1878) made important contributions, some reprinted by Sargent (1889), Graham (1972), and Stuckey (1978). The notes made by Gray in 1840 were in a book review written when he was only thirty years old. As early as 1859, Gray cited the work of Darwin and Wallace on natural selection and he stressed the effect of glaciation on present distribution. Li (1952, 1972), who knew both regions, made a detailed analysis and reviewed the extensive literature. He prepared worldwide maps showing outline ranges of many tree genera.

Atlases. Accurate distribution maps of most north temperate tree species have been published, replacing the general outlines by Schmucker (1942). No new maps are presented here. Worldwide generic maps have been compiled, especially by Li (1952) and by Meusel et al. (1965–78). Atlas of United States Trees (Little, 1971–81) in six volumes maps approximately 684 tree species native in continental United States including Alaska. The Forest Service Checklist of United States Trees (Little, 1979) further compiles for each of the 216 native genera the worldwide totals of species and their geographic extent, and cites authors of scientific names, omitted here. Native Trees of Canada (Hosie, 1979) similarly describes, illustrates, and maps the species of that country.

For Europe there are detailed maps of vascular plants of the northwestern part (Hultén, 1950), central region (Meusel et al., 1965–78), and the continent (Jalas & Suominen, 1972–80, incomplete).

Two volumes of an atlas of the trees and shrubs of the Soviet Union have appeared (Bot. Inst.

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Komarova, 1977). Maps for southwest Asia, or Asia Minor, are being published with financial assistance from the United States Public Law 480 program (Browicz, 1978). For Japan there are similar atlases of forest trees (Japan Forest Technical Association, 1964–71) and the flora (Hara, 1958–59; Horikawa, 1972–76).

Monographs. Additional information on distribution with species maps is available in current worldwide taxonomic monographs of north temperate tree genera. Examples are: *Abies* (Liu, 1971; supported by Public Law 480); *Aesculus* (Hardin, 1957, 1960); *Alnus* (Murai, 1964; Furlow, 1979); *Catalpa* (Paclt, 1952); *Cupressus* (Silba, 1981; Wolf & Wagener, 1948); *Illicium* (Smith, 1947); *Lyonia* (Judd, 1981); *Nyssa* (Eyde, 1966); *Osmanthus* (Green, 1958); *Pinus* (Mirov, 1967); *Sassafras* (Keng, 1953); and *Stewartia* (Spongberg, 1974). For *Pinus,* subdivisions as well as species have been charted (Critchfield & Little, 1966; Little & Critchfield, 1969). Other generic monographs cover geographic regions, such as North America.

Forestry. Deciduous hardwoods (dicotyledons) are important in forestry as well as horticulture. The Society of American Foresters at its annual meeting on Sept. 20–22, 1982 at Cincinnati, Ohio, stressed the main subject or theme: "America's Hardwood Forests—Opportunities Unlimited." Seeds and other germplasm are desired for tree breeding or genetics research programs. Eastern Asia is the world's largest and richest source of temperate deciduous hardwoods. Thus, many related species are available for introduction, selection, and hybridization. Also, Old World genera merit testing in new environments, hopefully pest-free, in the New World. Foresters are actively exchanging seeds, information, and expertise.

Relationships. Li (1952) observed that the floristic relationships are primarily generic and not specific. Recent work (such as that cited above) has resulted in the recognition of distinct species in the two geographical areas.

Tree Species in Both Temperate North America and Eurasia

Many species pairs of morphologically similar and apparently closely related tree species have been listed from Eastern North America and Eastern Asia. Li (1972) included examples from these tree genera: *Acer, Aralia, Cornus, Diospyros, Ilex, Rhus, Styrax,* and *Symplocos.*

At present only about five tree species of temperate North America are accepted as native also in Eurasia. Trees are conspicuously absent in long lists of plants on both sides of the North Atlantic Ocean (Hultén, 1958), lists of circumpolar plants (Hultén, 1971), and a list of plants in both Western North America and Japan (Mizushima, 1972). (However, several tropical species, especially mangroves and other beach plants of southern Florida, are common both to New and Old Worlds.)

Juniperus communis, common juniper, perhaps the tree species with greatest range in the world, is circumboreal or circumpolar, extending northward beyond the limit of trees. However, in the New World it is usually a low mat-forming shrub, rarely a small tree.

Two tree species of *Alnus,* alder, are widely distributed, though agreement on classification is lacking. *Alnus incana* of Eurasia has two New World varieties or closely related species: *A. rugosa* in northeastern North America and *A. tenuifolia* in northwestern North America. *Alnus sinuata,* often included in the shrubby species *A. crispa,* ranges from northwestern America into northeastern Asia. Also, two tree species of *Salix,* willow, *S. alaxensis* and *S. bebbiana,* extend from northwestern North America into northeastern Asia.

In the past, several other temperate North American tree species or their varieties have been recorded also from eastern Asia. Examples are *Acer rubrum, Alnus maritima, Cephalanthus occidentalis, Fraxinus nigra,* and *Ilex montana.* A few other paired species of *Ilex* are very closely related. *Styrax officinalis,* a tree species of the Mediterranean region, is represented in California by two shrub varieties, var. *californicus* and var. *fulvescens* and in western Mexico by var. *jaliscanus.*

Paleobotanical Evidence

Of course, the study of plant relationships must be based primarily upon the evidence of fossils. A new paleobotany text begins with this sentence: "The only method by which a history of the plant kingdom can be reconstructed is by a study of fossil plants found in the rocks of the earth" (Taylor, 1981: 1).

Paleobotanists are doing a fine job with the mostly incomplete specimens and disconnected scraps now available, though misidentifications have occurred. The work is slow, and the gaps seem almost insurmountable. Meanwhile, per-

haps others may be permitted to consider and evaluate additional lines of evidence for relationships and even to speculate. Unfortunately, some wild speculations have resulted, and the term "hysterical" plant geography has been proposed!

Briefly, the fossil record reveals a widespread occurrence of many modern genera of woody plants, designated as the Arcto-Tertiary flora, more or less uniform across the temperate lands of the Northern Hemisphere, from the close of the Cretaceous period through the Cenozoic Era, roughly 65 million years in duration. Many genera can be traced back that far, though their origins are obscure and the ancestries uncertain.

Western North America has a fossil plant record known in much greater detail than has Eastern North America. For example, Wolfe (1969) in a vegetational history of the Pacific Northwest recorded from the early and middle Miocene flora these 17 tree genera now absent but persisting in Eastern North America: *Carya, Castanea, Catalpa, Cladrastis, Clethra, Diospyros, Fagus, Gordonia, Gymnocladus, Halesia, Ilex, Liquidambar, Liriodendron, Magnolia, Nyssa, Sassafras,* and *Tilia.* Also, these genera now extinct in the New World: *Ailanthus, Cercidiphyllum,* and *Zelkova.*

About the middle of the Miocene epoch, some 15 million years ago, the climate became cooler and the components of the uniform Arcto-Tertiary forest began to migrate, with subsequent disassociations and extinctions occurring. At present, boreal temperate forests extend through land masses across northern North America and Eurasia. Their composition can be described in a very simplified way as follows: southward the forests separate into four main isolated forest regions or centers. Three regions now have the climate of deciduous hardwood forests with a long warm moist growing season and moist soil throughout the year. The fourth, Western North America, has other climatic patterns, such as dry summers, adapted to conifers. Eastern Asia is the geographic region or center with greatest display of the widespread Arcto-Tertiary flora, while Eastern North America is second, with roughly one-half as many tree species. Europe and Western North America have smaller numbers, perhaps one-fourth as many.

The presence and persistence of the Arcto-Tertiary flora and differences in present numbers of tree species in these regions are readily explained by movements of continental land masses unsuspected a century ago and by the continuation of a favorable climate in these regions. Pleistocene glaciation caused regional climatic changes that greatly influenced the distribution of these tree species. The deciduous forests of eastern Asia merged southward into evergreen tropical forests and apparently shifted downward with advances of continental ice sheets and lower temperatures. In eastern North America similar movements of forest zones southward have been documented by pollen analyses or palynology (Davis, 1969). However, the evergreen tropical forest is not continuous southward but is present in the West Indies and on mountains of Mexico and Central America. In southern Europe, the Alps and east-west mountain chains, as well as the Mediterranean Sea, served as barriers to the southward migration before glacial advances. Obviously, extinction of many tree species followed. In Western North America the climates following mountain-building were drier and unfavorable for survival of deciduous hardwoods except a few relicts (*Acer, Alnus*) in moist sites, such as valleys.

Patterns of Distribution

Four northern temperate forest regions can be designated by letter, from west to east (a fifth, the Colchic, from southeastern Europe to Iran, is not considered here): A, Western North America; B, Eastern North America; C, Europe; and D, Eastern Asia. There are 15 mathematically possible combinations: widespread in all four (ABCD), in three regions (ABC, ABD, ACD, BCD), in two regions (AB, AC, AD, BC, BD, CD), and endemic to one region (A, B, C, D). Three combinations, CD, C, and D, are exclusively Old World and omitted here. Three others, AB, A, and B, are New World endemics to be treated separately.

Many tree genera, some with numerous species common and dominant in temperate forests are widespread in all four regions or also beyond and have persisted in different climates (ABCD). Familiar examples, not considered further here, with reference by number to published generic maps by Meusel et al. (1965–78), are: *Abies* (map 20a), *Acer* (map 276b), *Alnus, Betula, Cornus, Crataegus, Fraxinus* (map 340b), *Juniperus* (map 22d), *Larix* (map 21a), *Picea* (map 20c), *Pinus* (map 21c), *Populus* (map 112b), *Prunus* (map 226c), *Quercus* (map 121c), *Salix* (map 112b), and *Sorbus.* A few others, such as *Aesculus, Cercis, Ostrya, Staphylea* (map 275d), and *Taxus*

TABLE 1. Tree genera (7) confined to Eastern North America (United States or also southeastern Canada) and Eastern Asia, with approximate numbers of species (BD). Maps by Li (1952) are cited by number.

Genus	World Total	Eastern North America	Eastern Asia
Chionanthus[a] (map 42)	3	2	1
Cladrastis (map 26)	4	1	3
Gymnocladus (map 25)	4	1	3
Halesia (map 41)	4	3	1
Liriodendron (map 12)	2	1	1
Sassafras (map 16)	3	1	2
Stewartia (map 31)	10	2	8
Totals	30	11	19

[a] The related genus *Linociera,* if united, would add 80–100 species, mostly tropical and subtropical, and cause removal from the list.

(map 19d), have mostly restricted occurrence in the four regions with partly relict species.

The eight remaining combinations involve one or both North American regions with one or both Old World regions. Tree genera under different patterns, with approximate numbers of species, are presented in Tables 1–5. The well-known pattern of Eastern North America and Eastern Asia (BD) is represented by the most tree genera, about 15 (Tables 1 and 2). This group can be divided into two, one extending beyond southward into subtropical regions, such as West Indies and mountains of Mexico and Central America and in southeastern Asia to Indonesia. Pattern BCD has eight genera (Table 3), ABD has five (Table 4), and AD has four (Table 5). Patterns ACD and AC apparently have a single tree genus each, while ABC and BC have none.

Cupressus, cypress, apparently is the only tree genus absent from Eastern North America (ACD) but present in the other three regions. There are eight species in Western North America, including one from Mexico to Honduras, one in the Mediterranean region, and six in eastern Asia, mainly China.

Arbutus, madrone, is limited to two warm temperate regions, Western North America and Europe (AC; map 329c). There are eight or fewer species in Western North America south to Mexico (one to Nicaragua) and about ten others in the Mediterranean region of Southern Europe and Western Asia.

Table 1 summarizes tree genera confined to Eastern North America (United States or also southeastern Canada) and eastern Asia (BD). All seven genera of mostly deciduous hardwoods are small with relatively few species. Cain (1943) observed that these ancient groups were well displayed as relicts in coves, or rich moist valleys of the Southern Appalachians. Li (1952) noted also two paired genera: *Taxodium* with three (or two) species in Eastern North America (one south to Guatemala) and *Glyptostrobus* with one in China; and *Elliottia* with one species very rare and local in Georgia and *Tripetaleia* with two shrub species in Japan (map 36).

TABLE 2. Tree genera (9) confined to Eastern North America and also south to mountains of Mexico, Central America, or West Indies and to Eastern Asia, with approximate numbers of species, including a few shrubs (BD+). Maps by Li (1952) are cited by number.

Genus	World Total	Eastern North America	Mexico, Central America (additional)	West Indies	Eastern Asia
Carya (map 2)	16	11	1		4
Catalpa (map 46)	11	2		5	4
Gordonia (map 32)	31	1			30
Hamamelis (map 23)	6	2	1		3
Illicium (map 14)	42	2	1	2	37
Lyonia (map 32)	35	5	1	24	5
Magnolia (map 13)	76	8	10[a]	8	50
Nyssa (map 35)	5	3			2
Osmanthus	32	1	1		30
Totals	254	35	15	39	165

[a] To Ecuador in northern South America.

TABLE 3. Tree genera (8) of Eastern North America and in both Europe and Eastern Asia but now absent from western North America, with approximate numbers of species (BCD). Maps by Meusel et al. (1965–78) are cited by number.

Genus	World Total	Eastern North America	Europe	Eastern Asia
Carpinus (map 117d)	28	1	2	25
Castanea (map 121b)	12	4	1	7
Cotinus (map 273d)	4	1	1	2
Fagus (maps 120c, 121a)	10	1	2	7
Liquidambar	3	1	(1)[a]	1
Pistacia (map 274a)	10	2[b]	3	5
Tilia (map 280c)	29	4	5	20
Ulmus	46	11[c]	5	30
Totals	142	25	20	97

[a] Southwestern Asia.
[b] One in southern Texas and northeastern Mexico and one in Mexico and Guatemala.
[c] Includes five species in Mexico, one also to Panama.

Table 2 has nine genera of mostly deciduous hardwoods of slightly broader distribution in the same regions (BD+). These genera are mainly small and in the Old World, though *Carya* is better represented in the New World. From Eastern North America one or more species range southward in tropical mountains to Mexico or Central America and/or West Indies. *Magnolia* reaches Ecuador. Distribution in Eastern Asia is greater, projecting southward into tropical mountains to Indonesia.

Table 3 has eight genera mostly widespread across the deciduous forests of the Northern Hemisphere (BCD). They are now absent from Western North America, which currently lacks a deciduous forest climate but were present there in the Miocene. Some species extend slightly southward, such as to Mexico or Panama or to northern Africa or southwest Asia. Largest numbers of species are in Asia. *Buxus* (Meusel et al., 1965–78, map 273b) might be added, with New World species in the West Indies, Mexico, and Central America, though absent northward.

Table 4 has five small genera absent from Europe (ABD). The four genera of conifers were named from Eastern North America and afterwards found in the other regions and were present in Western Europe in the Miocene and Pliocene.

Table 5 has only four genera, which are confined to the arc around the North Pacific Ocean and which may not have been widely distributed in the past (AD). Three genera are mostly broadleaved evergreens of subtropical and tropical

TABLE 4. Tree genera (5) of both Western and Eastern North America and Eastern Asia but absent from Europe, with approximate numbers of species (ABD).

Genus	World Total	Western North America	Eastern North America	Eastern Asia
Chamaecyparis	6	2	1	3
Thuja	6	1	1	4
Torreya	6	1	1	4
Toxicodendron[a]	16	1	5[a]	10
Tsuga	14	2	2	10
Totals	48	7	10	31

[a] Includes shrubs and woody vines and one tree species from Mexico to Brazil.

TABLE 5. Tree genera (4) confined to Western North America and Eastern Asia with approximate numbers of species (AD). Maps by Meusel et al. (1965–78) are cited by number.

Genus	World Total	Western North America	Eastern Asia
Castanopsis[a] (map 121b)	102	2	100
Lithocarpus (map 121b)	101	1	100
Photinia[b]	61	1	60
Pseudotsuga	6	2	4
Totals	270	6	264

[a] Includes one tree and one shrub species in North America also placed in the segregate genus *Chrysolepis*.
[b] The one species in North America also placed in the segregate genus *Heteromeles*.

range in Eastern Asia with a single tree species disjunct in Western North America. Minor differences have been noted. Thus, the segregate genus *Chrysolepis* Hjelmqvist (1948) has been proposed for the two New World species of *Castanopsis*. The segregate genus *Heteromeles* M. J. Roem. (1847) is now generally adopted for the single New World species also united under *Photinia*. *Calocedrus*, if accepted as a segregate from *Libocedrus* (about ten species), would be added to Table 5, with one New World species and two Old World. Genera of deciduous trees are absent.

ENDEMIC TREE GENERA

About 23 additional tree genera (discussed below) are now endemic to temperate North America (Little, 1979: 16–19). Some are old and relicts of wider fossil occurrence also in Eurasia, while others may be young. Several others of southern and southwestern United States not mentioned here are subtropical or tropical in origin.

About eight genera that include at least one tree species have natural ranges confined to western North America (A), most with only one or two species, and centering in California, part coastal and subtropical. They are: *Adenostoma*, two species, also in Baja California, Mexico; *Cercocarpus*, six species, about four additional in Mexico; *Fremontodendron*, two species, also in Baja California; *Heteromeles*, one species, often united under *Photinia*, also in Baja California; *Lyonothamnus*, one species, confined to four California islands; *Oemleria* (*Osmaronia*), one species, north to British Columbia; *Sequoia*, one species; and *Sequoiadendron*, one species, segregated from *Sequoia* in 1939.

About 11 genera that include at least one tree species have natural ranges limited to temperate eastern North America (B; Little, 1980). Most are restricted to the United States and have only one species. They are: *Asimina*, eight species, one species extends north to extreme southern Canada; *Cliftonia*; *Elliottia* (the closely related genus *Tripetaleia* with two species in Japan); *Franklinia* (extinct except in cultivation); *Leitneria*; *Maclura*; *Nemopanthus*; *Oxydendrum*; *Pinckneya*; *Planera*; and *Taxodium* (which was widespread in the Arcto-Tertiary province from the Cretaceous on into the Pliocene), two species, one south to Guatemala.

Leitneria with one relict species is in the distinct family Leitneriaceae. Tertiary fossils from Mississippi, Oregon, and western Siberia have been referred here. *Maclura* would not be endemic, if the related genus *Chlorophora* of tropical America and Africa or an Asian genus were united.

Three tree genera have broad natural ranges in temperate North America, both eastern and western (AB) and south into Mexico. *Garrya*, often placed in a separate family Garryaceae, has 14 species of shrubs and trees, mostly in western United States and Mexico, including one south to Panama, also one in the Greater Antilles (Dahling, 1978). This genus with a fossil record back to Miocene apparently originated in the Southwest. *Ptelea* has three species, one in Mexico only (Bailey, 1962), and is recorded back to Eocene in western and eastern states and to Oligocene in Europe. *Robinia* has about ten species including shrubs, mostly eastern, one in Mexico only. Fossils have been referred to this genus in North America and Europe back to Paleocene and in Japan to Miocene.

Young genera. Two endemic tree genera, one western and one eastern, apparently are young and lack a fossil record. *Oemleria* (*Osmaronia*) with one species may have originated from *Prunus*, a genus with about 33 species of trees and shrubs native across North America and 200–400 worldwide. *Oemleria cerasiformis* is a shrub or rarely small tree occurring in mountain canyons from California north to British Columbia. *Oemleria* differs from *Prunus* in having usually five pistils instead of one, flowers unisexual as well as bisexual, and leaf margins entire rather than serrate.

Nemopanthus may have evolved from *Ilex*. The latter has about 15 species in Eastern North America, is extinct in the western part, and is widespread with 300–350 species mostly tropical (Meusel et al., 1965–78, map 274). *Nemopanthus mucronatus* is a shrub or rarely small tree of northeastern United States and southeastern Canada, along and mostly north of the range of *Ilex* in the glaciated region. The relatively new, glaciated land and the habitat of wet soil of bogs and swamps would aid a new, pioneer species. *Nemopanthus* differs from *Ilex* in slight flower characters: petals distinct instead of united at base, stamens free and distinct rather than inserted on corolla, and calyx-lobes none or minute. A second species transferred from *Ilex* is controversial, as are three Old World fossils placed here more than a century ago.

Will it be possible to observe the origin of the next new genus of North American trees? One

species of *Abies* local in the Santa Lucia Mountains of Central California merits watching. H. L. Mason in a paper at a scientific meeting in 1957, predicted that this species would be named a new genus. This distinct species at the border of the generic range is so different from all the other 38 species of *Abies* worldwide that it has been placed alone in a second subgenus, *Pseudotorreya.* Interestingly, it has been classed also as the most primitive species (Liu, 1971).

Subdivisions of Genera

Studies of relationships between tree genera of these four separate regions commonly do not extend to the subdivisions, perhaps partly because of difficulties in classification of fossils. However, living or recent species show various patterns of distribution. A good example is the genus *Pinus,* pine, which has about 95 species of wide range in north temperate regions and southward in tropical mountains. It has a fossil record back to early Cretaceous and Jurassic periods (Mirov, 1967: 106). Also, its subdivisions as well as species have been mapped (Critchfield & Little, 1966; Little & Critchfield, 1969). The two main subgenera, *Strobus* or soft pines and *Pinus* or hard pines, are widespread, and their four sections also in both Old and New Worlds. However, the 15 subsections are more restricted, only three in both but four Old World and eight New World. These 15 subsections may be grouped as designated above by letters as: ABCD, 1 subsection; ACD, 1; BCD, 1; AB, 1; A, 6; B, 1; CD, 1; C, 1; D, 2.

The genus *Pinus* apparently originated in temperate Eastern Asia. The large number of species centering in Mexico indicates a center of speciation in the Tertiary. *Pinus* subsect. *Cembrae* (ACD) is represented by five species of high altitudes and northern latitudes but is absent from Eastern North America, which lacks high mountains (Little & Critchfield, 1969, map 4). *Pinus albicaulis,* whitebark pine, is a timberline tree of the northern Rocky Mountains and the only New World member of the group. *Pinus cembra,* Swiss stone pine, grows at high altitudes in the Alps and Carpathian Mountains of southern Europe. The other three species are Asian: *P. sibirica,* Siberian stone pine, mostly in western and central Siberia; *P. pumila,* Japanese stone pine, from northwestern Asia to Japan; and *P. koraiensis,* Korean pine, from Korea to southeastern Siberia and Japan. This subsection has been regarded as one of the most primitive in the genus and is characterized by a closed cone.

Of similar distribution is a genus of birds, *Nucifraga,* related to jays and crows. These birds break open the cones and store and eat the large wingless seeds of sect. *Cembrae*, thus aiding dispersal. The New World species is *N. columbiana,* Clark's nutcracker or Clark's crow ("camp-robber"), and the Old World species is *N. caryocatactes,* European nutcracker, with ten named subspecies or races (Goodwin, 1976). Obviously, both pine and bird groups were present together in the ancestral Arcto-Tertiary forests and may have evolved in symbiosis. Both bird species have a somewhat varied diet including other seeds, berries, insects, and eggs and readily learn to eat foods of humans.

The disjunct genus *Magnolia* has eight species in eastern United States, about 18 others southward in tropical America, and about 50 in Eastern Asia south to Java (Little, 1971). Seven of the 11 sections of the genus are entirely Asian, two are wholly American, and two occur in both regions. Nine sections are confined to a single region.

The eight species of *Magnolia* in eastern United States are classified in four sections. *Magnolia acuminata* and a species of eastern China are in sect. *Tulipastrum,* sometimes treated as a genus. Two of the southern Appalachians, three of the Coastal Plain, and one of Mexico are placed with three of Asia in sect. *Rytidospermum. Magnolia virginiana* is sufficiently distinct to be alone in sect. *Magnolia. Magnolia grandiflora* of the southeastern Coastal Plain is the northern outpost of sect. *Theorhodon,* composed of about 16 evergreen tropical species south to Puerto Rico, the ancient flat-topped peaks of southeastern Venezuela, and Ecuador. All species of the last section may have evolved from the same New World ancestor.

Alnus, alder, is another illustration with widespread subgenera. *Alnus maritima* has an odd range in two areas more than 1,800 km distant: Coastal Plain in five counties of eastern Maryland and one in southern Delaware and stream banks on granite bedrock in two counties of southern Oklahoma. This pioneer species in wet soil bordering water is regarded as a relict of former wider range with the Oklahoma area the older of the two (Furlow, 1979: 17). It is the only New World representative of *Alnus* subg. *Clethropis,* which ranges also from Himalayas to Japan and as fossil records in Western North

America. *Alnus japonica* of Japan has been treated as a variety.

TREES OF WESTERN AND EASTERN NORTH AMERICA

Relatively few tree species confined to North America have broad east-west ranges and can be classed as transcontinental. Examples are mostly species of wide occurrence in the northern coniferous forest, such as *Picea glauca, Larix laricina, Populus tremuloides,* and *Betula papyrifera.* Southward, the few tree species that are found across the treeless interior commonly grow in moist soil near water, for example, *Salix nigra* and *Acer negundo.*

Every field botanist traveling for the first time from Eastern to Western North America (or the reverse) has observed the striking resemblance of various trees and other plants to species previously studied. These similar plants are known as paired species, parallel species, species pairs, east-west vicarious taxa, and east-west vicariads. More than two species may be involved. Long lists of these species pairs have been compiled (Wood, 1971).

A few examples of tree species pairs may be noted, the western first: *Pinus monticola* and *P. strobus, Juniperus scopulorum* and *J. virginiana, Quercus gambelii* (also *Q. lobata* and *Q. garryana*) and *Q. alba, Celtis reticulata* and *C. occidentalis,* and *Acer grandidentatum* and *A. saccharum* (also *A. nigrum* and *A. barbatum*).

The explanation is obvious. The western and eastern forests became separated and isolated following western mountain uplifts and the origin of drier interior plains with grassland vegetation in late Miocene and early Pliocene more than five million years ago. One or both species of the pair changed during the interval though not into a distinct genus.

RELICT SPECIES

Some tree species of disjunct genera appear to be old and relict and declining, often rare. However, *Liriodendron tulipifera* and *Sassafras albidum* of Eastern North America are widespread and common. They are also the northernmost members of their families, Magnoliaceae and Lauraceae. Many species of conifers are rare or local in North America. Thirty-five, mostly western, have been the subject of a special publication with maps (Little, 1975).

Examples of relict tree species in Eastern North America with published maps (Little, 1971–81, vol. 4) include: *Cladrastis kentukea* (map 35); *Cotinus obovatus* (map 46); *Illicium parviflorum* (map 73); *Leitneria floridana* (map 74); and *Stewartia ovata* (map 147). Four tree species are endemic to islands of California, for example, *Lyonothamnus floribundus* (vol. 3, map 98) representing an endemic genus.

General observations made earlier on the ecology of rare plants may apply also to many examples of disjunct genera and species. Griggs (1940) concluded that a species is rare because it cannot compete successfully with common plants, that most rare species have habitats in the early stages of the ecological succession, and that many rare plants have disrupted ranges and are slowly dying out. Examples of trees characteristic of dry rock outcrops in the upland succession are *Cotinus obovatus* and *Torreya taxifolia* (Little, 1971–81, vol. 1, map 88-E). Trees of wet soil of stream banks in the lowland succession include *Leitneria floridana* (vol. 4, map 74) and *Alnus maritima* (vol. 4, map 8).

Minor geographic variations may be expected among isolated populations of ancient taxa. Most careful studies of conifers have revealed additional differences. In observing conifers for many years, I have noted some local variations and have named a few. Opinions disagree whether the differences should be designated as varieties or species or left unnamed. An extreme example is the genus *Cupressus,* cypress, which has been mentioned. As many as 15 New World species have been accepted, mostly with separate ranges (Wolf & Wagener, 1948). However, I distinguish only eight species, subdivided further into ten geographical varieties (Little, 1975, plate 9, maps 29–35). The species and varieties in western United States have ranges so local and disjunct that the isolated stations for each species have been counted. Clearly, these are relicts of former greater occurrence.

DISCUSSION

Several observations are offered here. My interest in this subject goes back to a fascinating graduate course in floristics by an inspiring professor, Henry Chandler Cowles, at the University of Chicago (1927).

Progress in geology. Historical plant geography has kept pace with progress in geology. When I studied historical geology (1925), there was no precise time scale in millions of years. In

structural geology (1926), I was taught that continents and ocean basins were fixed and that continents moved up and down vertically (isostasy) but never horizontally. Alfred Wegener's hypothesis of continental drift proposed in 1915 did not come to the attention of plant geographers until later. I recall an introduction to the subject by Wendell H. Camp at a field meeting of botanists in 1939. Some botanists readily grasped movement of continents as more plausible than land bridges. Others hesitated momentarily, because physicists had no explanation or because the hypothesis seemed unnecessary. Now, continental movements provide an explanation for some problems of plant distribution! Recent acceptance of wandering poles will lead to additional explanations and may require revision of paleogeographic maps. The shift in pole position and earth's axis within the past 80 to 100 million years is estimated at about 20 degrees latitude (Good, 1964; Harrison & Lindl, 1982).

Time. One important concept in studies of plant geography is time. A century ago James (1881: 67) observed "that the time necessary for the distribution of our plants has been sufficiently long." He concluded also that the species of plants common to Europe and America had a common origin and migrated south. Time has been sufficient for many tree species to migrate to the most remote part of the earth wherever conditions for establishment are suitable. It is difficult to conceive of continuous time longer than the few thousand years of written history.

However, the time since the beginning of the Tertiary period, about 65 million years, is adequate to explain present distribution of trees and other seed plants throughout the world wherever there are suitable habitats. The time is ample for migration by any means, gradual, in steps, or by accident in long distance dispersal. Of course, continental movements speed the process.

Change. A key word in studying plant distribution is change, or dynamics. Just as all organisms end in death, all species become extinct or change into others by evolution. Likewise, the natural distribution of a species is slowly changing.

Persistence of tree genera. It seems remarkable that many extant or recent tree genera can be traced back as much as 50 million years into the Eocene epoch or doubtfully farther into the Cretaceous period. That is a very long time for a genus to maintain its identity and to continue to be common and widespread. In contrast, evolution of land vertebrates has been more rapid. Within the same time interval, *Equus,* the modern horse, developed from the 4-toed ancestral dawn horse, *Hyracotherium* (*Eohippus*). Even after separation of the land masses and forest regions in the Miocene roughly 15 million years ago, the tree genera in isolation maintained their identity. Obviously, these old tree genera are stable and have a slow rate of evolution.

Trees and herbs compared. Herbaceous plant species are considerably more numerous than trees in temperate regions though not as well preserved in the fossil record. Also, herbaceous species of wide distribution in temperate regions in both New and Old Worlds are much more numerous than trees, as noted above. However, many of the herbs are circumpolar across far northern regions above the tree line or climatic limit of trees. Thus, it appears that herbs have a more rapid rate of evolution than trees and that herbs migrate faster. Herbs have much shorter life cycles and more numerous generations and mostly small seeds adapted to long distance dispersal. While one seedling in many years replaces a tree, an annual herb is followed by another plant each year.

Conclusions. The relationships of North American trees with Eastern Asia have been overemphasized and are readily explained by earth changes accepted within recent years.

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